

# Post-fire succession on savanna habitats in the Okavango Delta wetland, Botswana

Michael Heinl<sup>\*,†,1</sup>, Jan Sliva<sup>†</sup>, Michael Murray-Hudson<sup>‡</sup> and Budzanani Tacheba<sup>‡</sup>

\* Institute of Ecology, University of Innsbruck, Sternwartestr. 15, A-6020 Innsbruck, Austria

† Chair of Vegetation Ecology, Munich University of Technology (TUM), D-85350 Freising-Weihenstephan, Germany

‡ Harry Oppenheimer Okavango Research Center (HOORC), University of Botswana, Maun, Botswana

(Accepted 13 July 2007)

**Abstract:** Drying floodplains that were not inundated for more than 10 y were investigated to relate plant species and vegetation structure to time-since-fire for the southern Okavango Delta wetland in Botswana. The aims of the research were to study post-fire succession on savanna habitats in the Okavango Delta and to investigate the mechanisms behind vegetation changes with time-since-fire. We hypothesize that vegetation structure rather than species occurrence is affected by the fire event and that the driving forces of post-fire succession change from fire-driven to competition-driven with increasing time-since-fire. A total number of 153 study sites were investigated, representing areas of 2–12 y without a fire. Both woody and herbaceous plant species were recorded and cover/abundance values were measured. The vegetation changes with time-since-fire could be assigned to three different successional stages: (1) the post-fire conditions shortly after fire, supporting high species numbers due to open space and little competition; (2) the dominance of competitive perennial grass species (e.g. *Urochloa mosambicensis*) after 6–8 y; and (3) the enhanced establishment of woody species after about 10 y, creating new habitats in their vicinity. High species numbers were found after short and long fire-free periods, and different species occurred shortly after the fire event and at late stages of the post-fire succession. A variety of different inter-fire intervals is therefore expected to be responsible for sustaining plant species richness and habitat diversity in the study area. Post-fire succession could be described as not only being driven by the life history of the species, but also by seedbank dynamics and plant mobility in early successional stages and by competition and niche differentiation in late-successional stages.

**Key Words:** fire, fire ecology, fire history, fire regime, richness, southern Africa, structure, vegetation

## INTRODUCTION

Vegetation fires are common phenomena in almost all parts of southern Africa and are considered determinants of vegetation structure and plant diversity in a multitude of different landscapes (Bond & van Wilgen 1996, DeBano *et al.* 1998). The specific impact of fire varies with the fire regime and the vegetation type affected.

A combination of fire frequency, fire intensity and fire season is usually considered to constitute a fire regime. These fire parameters describe in principle how hard the vegetation is or can be 'hit' by the fire. The maximum temperatures reached and their duration during the fire, the ability of the vegetation to cope with disturbances, or the stage of the plant species in their life history very much

determine the severity of the impact on the vegetation by the fire (Andersen *et al.* 1998, Bond 1997, Bond & van Wilgen 1996, Booysen & Tainton 1984). Hence, the knowledge of the fire parameters can, in principle, be used, in combination with the understanding of the ecology of the plants affected by the fire event, to estimate mortality or recovery of the vegetation after fire. Post-fire succession is very much determined by the situation after the fire event, i.e. by the survival of specific species and by the post-fire condition. These factors set the 'starting point' after the disturbance event. But the influence of the fire parameters on vegetation should become less pronounced with increasing time-since-fire. The determinants of the successional pathway should change with time from fire-dependent to density-dependent.

Assessing vegetation changes in a time-since-fire framework investigates the successional development after fire, but cannot consider either the fire event or

<sup>1</sup> Corresponding author. Email: michael.heinl@uibk.ac.at

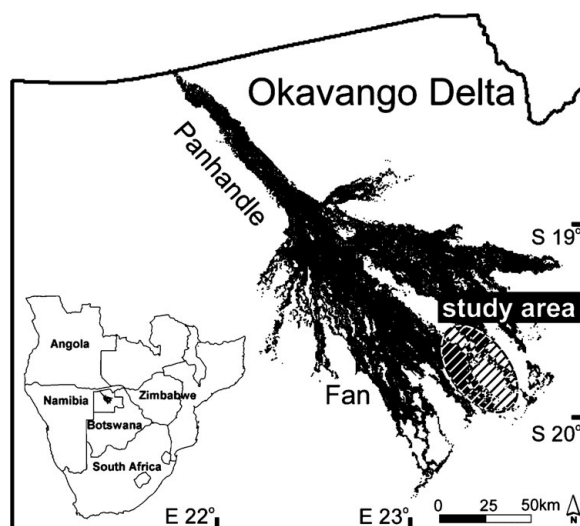
the length of the inter-fire interval (Morrison *et al.* 1995). Changes after a fire are therefore expected to reflect a typical development between two fire events for an investigated vegetation type. Therefore, while working with fire regimes produces a rather static picture of a typical vegetation type associated with a specific disturbance regime, assessing vegetation response to time-since-fire analyses the changes and development between these disturbance events.

Post-fire succession is determined not only by the fire parameters, but is complicated by numerous other factors, such as pre-fire species composition and vegetation structure, weather patterns or herbivory. Thus, the specific change of certain communities with time-since-fire is not predictable and differs clearly from site to site. The present study therefore focuses on the determination of general trends of savanna vegetation related to time-since-fire, and specifically on vegetation structure and species attributes rather than on species assemblages and plant communities. Another focus is set on investigating the importance of fire events for species richness and on the driving forces in post-fire succession. We hypothesize that vegetation structure rather than species occurrence is affected by the fire event and that post-fire succession is increasingly driven by competition with increasing time-since-fire. Hence, the aims of the study are to enhance the understanding of the succession after fire events specifically on drylands in the Okavango Delta and savanna habitats and to investigate the mechanisms behind changes in species composition and vegetation structure with time-since-fire.

## METHODS

### Study area

The Okavango Delta in northern Botswana is a large tropical wetland in the centre of the Kalahari region. The world's largest site protected under the Ramsar Convention on Wetlands is supplied by the Okavango River and consists of a mosaic of temporary, seasonal and permanent wetland habitats and drylands over an area of approximately 15 000 km<sup>2</sup>. The Okavango Delta is an alluvial fan with a very low gradient of roughly 1:3300 (McCarthy *et al.* 2000), divided by geological fault-lines into the northern Panhandle and the unconfined Fan in the south-east (Figure 1). The Panhandle region can be described as a permanent swamp, with water supply by the Okavango River throughout the year. It is characterised by extensive monodominant *Cyperus papyrus* authority stands. With the drop of confining fault-lines, the water of the Okavango River spreads and forms the Fan of the Okavango Delta. The intensity of the flooding decreases towards the distal reaches of the Fan,



**Figure 1.** Location of the study area in the southern floodplains of the Okavango Delta wetland, northern Botswana.

so that this area is characterised by seasonal swamps, floodplains and drylands.

The focus of the present study is on drying floodplains of the Okavango Delta, which are today basically unaffected by floodwaters or only inundated during years with exceptionally high floods. While active floodplains are typically dominated by sedges like *Schoenoplectus corymbosus* and *Cyperus articulatus*, these drier habitats are usually characterized by grasses, mainly *Urochloa* sp., *Eragrostis* sp. or *Aristida* sp. The irregular flooding also allows woody species to establish (e.g. *Acacia* sp., *Combretum imberbe*, *Pechuel-loeschea leubnitziae*, *Colophospermum mopane*) (Ellery & Ellery 1997).

All these habitats are susceptible to fire, especially during the dry season with the highest fire activity around September (Heinl *et al.* 2007a). Recent studies have shown mean fire return intervals for drying floodplains of about 7–8 y (Heinl *et al.* 2006). Most of the fires in the Okavango Delta are thought to have an anthropogenic origin today. Reasons for burning are various and include land clearing for cultivation, stimulating grass growth for grazing animals and hunting or to improve access to fishing grounds etc. Accidental fires can be caused by camp fires or fish-smoking.

The specific study sites for this research are situated on typical savanna habitats in drying floodplains of the southern Okavango Delta (Figure 1) in Wildlife Management Areas with no agricultural land use or livestock grazing. The study sites were chosen based on their flood history and the elapsed time since the last fire.

### Site selection and sampling methods

The selection of specific study sites was based on previous studies on the fire and flood history of the southern

Okavango Delta (Heinl *et al.* 2006, 2007a). Analyses of a series of 98 Landsat satellite images from 1989 until 2003 provided data on fire occurrences and inundated areas, which were used to identify target sites according to flood history and time-since-fire.

For the present study, only drying floodplains were investigated, as they provide sufficient variety in time-since-fire and show no differences in the flooding regime. The investigated areas were all recorded as flooded at least once between 1989 and 2003, and were therefore considered as floodplains. But to qualify as drying floodplains, only those floodplains were selected that were not flooded after 1993. Hence, for all study sites inundation was only recorded between 1989 and 1993.

For these drying floodplains, study plots were selected representing 2 y since the last fire (15 sites), 4 y (75 sites), 6 y (6 sites), 8 y (20 sites), 10 y (20 sites) and 12 y (17 sites) since the last fire (space-for-time substitution). The difference in the number of samples was due to inaccessibility of relevant study areas. The number of years since the last fire is consistent with the number of growing seasons that have passed since the last fire. Hence, study plots that were investigated 2 y after fire were burned in 2002 and vegetation growth was in early 2003 and 2004.

The vegetation survey was performed in February 2004 and 153 study sites were investigated. For each site, a 10 × 20-m plot was established. On each plot, all woody species were recorded and abundance was counted. Additionally, aerial cover for each woody species was estimated using the scale after Londo (1984). In one corner of each 10 × 20-m plot, a 2 × 2-m subplot was established. On these subplots, both woody and herbaceous species were recorded and their aerial cover was estimated (scale after Londo 1984). Nomenclature of the plant species is after Arnold & De Wet (1993). Above-ground biomass (excluding litter) was collected inside each plot on a 50 × 50-cm sampling quadrat and weighed after drying at 85 °C for 24 h.

### Data analysis

For analysing the development of cover values of single species in relation to time-since-fire, the ten most abundant herbaceous species in the study, each recorded for at least 30 plots, were used. The species were visually classified into four groups according to the development of their cover values with time-since-fire. Plant traits of the selected species were assessed to allow the assignment of species life history to these four groups (Gibbs-Russell *et al.* 1990, Flora Zambesiaca online available at <http://www.kew.org/floras/fz/intro.html>, van Oudtshoorn 1999). To specifically analyse fluctuations in vegetation cover and total species numbers with time-since-fire

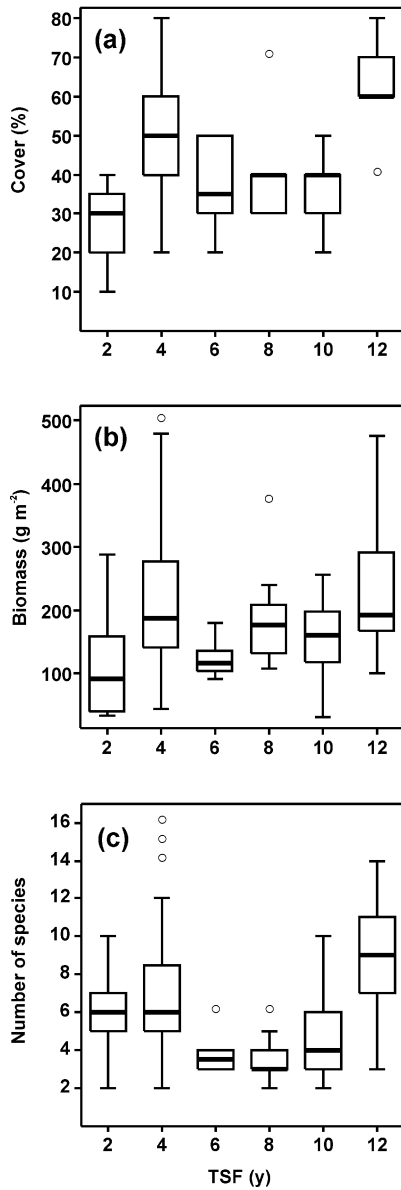
relative to the situation 2 y after the fire event, the complete species pool was split into initial species and successional species. Initial species were defined for the present study as all species that were recorded on plots representing 2 y after a fire event, while all other species were defined as successional species. To correct total species numbers for differences in sample size, rarefaction estimates were calculated and adjusted to the smallest sample size for initial and successional species, i.e. 13 and 10 subsamples, respectively (Krebs 1999, Rarefaction Calculator available at <http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>). Error estimates of mean values are presented as ± 1 SD. The non-parametric Mann–Whitney U-test was used to test the differences of samples for significance. Spearman rank correlation was used to assess correlations between cover values of selected species and species numbers.

## RESULTS

### The relation of the herbaceous layer to time-since-fire

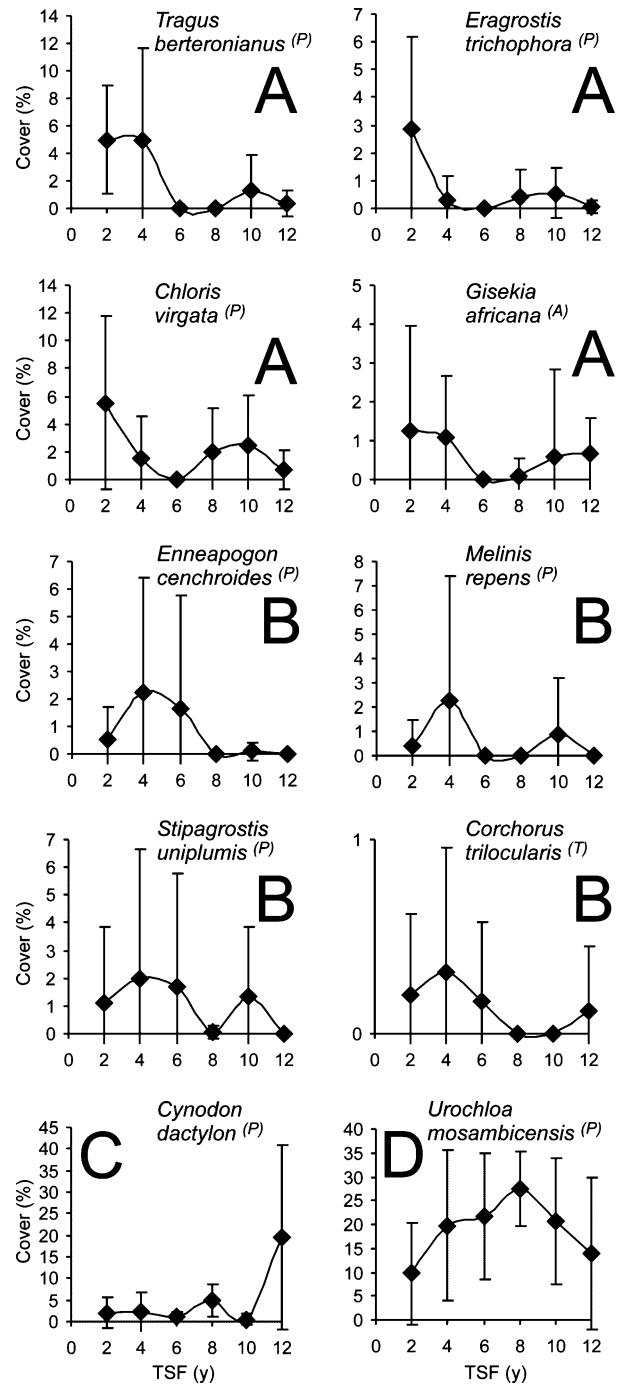
Analyses of the herbaceous layer showed both for total vegetation cover and above-ground living biomass an increase with time-since-fire (Figure 2). The mean values indicate a slow recovery immediately after the fire with only 27.3% ± 11.0% vegetation cover and 113 ± 83.7 g m<sup>-2</sup> above-ground living biomass after 2 y. The mean values were significantly higher after 12 y without fire and almost double to 62.9% ± 10.5% cover and 227 ± 93.7 g m<sup>-2</sup> biomass (U = 4.0, P < 0.001 and U = 42.0, P < 0.001, respectively). The mean number of species per plot was 6.0 ± 1.9 in the second year after fire and declined significantly with time-since-fire to only 3.6 ± 1.0 species per plot after 8 y without fire (U = 38.0, P < 0.001; Figure 2). Highest mean species numbers were found after 12 y without fire with 8.6 ± 3.3 species per plot.

Analysing the development of the cover values of the ten most abundant herbaceous species in the study in relation to time-since-fire revealed four different trends, which were grouped in A, B, C and D (Figure 3). The assessment of plant traits of these species led to the assignment of different life history to these groups. Group A consists of annual and typical pioneer species that establish quickly in disturbed places. *Tragus berteronianus* and *Eragrostis trichophora* have highest cover values immediately after the fire event and low cover values on plots with more than 4 y since the last fire. They thus show an obvious dependence on disturbance events. Similar effects are observable for *Chloris virgata* and *Gisekia africana*, but less pronounced. Species in Group B are short-lived perennials, although *Enneapogon cenchroides* and *Melinis repens* are also described as annual and



**Figure 2.** Total vegetation cover (a), biomass (b) and total number of species (c) related to time-since-fire (TSF). Presented are median values (central line), first and third quartiles (box), minimum and maximum values (whiskers) and outliers (circle).

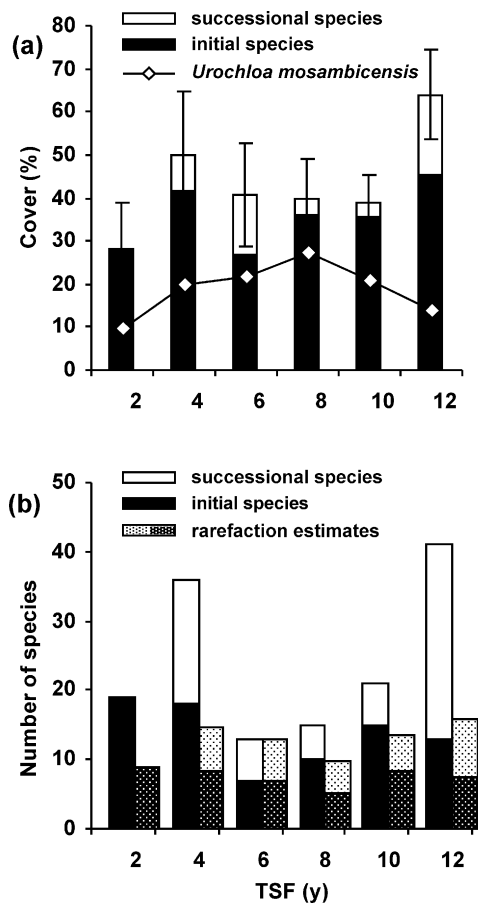
*Stipagrostis uniplumis* as subperennial. However, their life history under prevailing conditions seems to be longer than that of species in Group A and the pioneer character of these species is less pronounced, as they are almost absent in the first years after the fire-event. Group C is represented by *Cynodon dactylon*, typically perennial with rhizomes. The data suggest that more than 10 y without fire are needed for *Cynodon dactylon* to spread extensively, although a clear trend towards a steady increase with time-since-fire cannot be derived for this species. Group D is represented by *Urochloa mosambicensis*, also typically



**Figure 3.** Mean cover values of the ten most abundant herbaceous species in the study related to time-since-fire (TSF). The species are grouped according to their life history, indicated by the letters A, B, C and D (see text for details). Families are indicated by the letters after the species names (A: Aizoaceae; P: Poaceae; T: Tiliaceae). The error bars show ± 1 SD.

perennial, and shows maximum cover values about 8 y after the fire event.

The analyses of the life history of the most abundant species revealed a general trend of more annual and



**Figure 4.** Mean cover values (a) and total number of species (b) for initial and successional species related to time-since-fire (TSF). Initial species are species recorded only on plots that represent 2 y since the last fire. All other species are classified as successional species. Error bars show  $\pm 1$  SD of the mean cover values. Data for *Urochloa mosambicensis* are transferred from Figure 3. Rarefaction estimates for the number of initial species and successional species are added to account for differences in sample size (Krebs 1999).

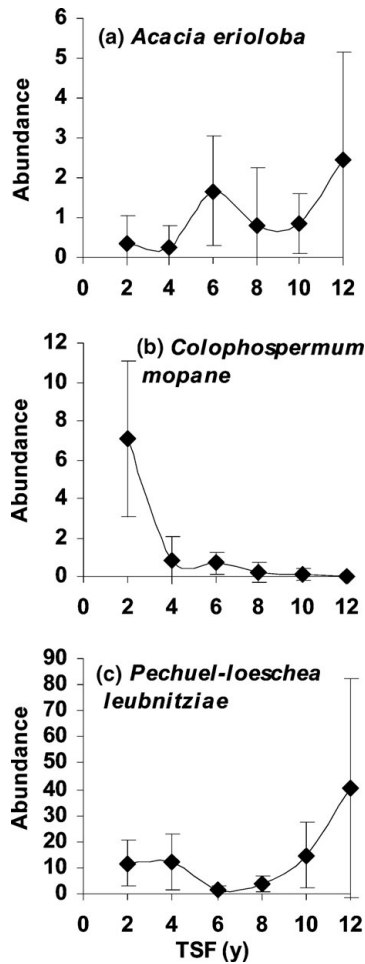
short-lived species shortly after the fire and a decline of these species with time-since-fire. However, as these are the most common species, they are present for almost all time-since-fire categories and do not contribute to the observed changes in the species numbers with time-since-fire (Figure 2). To analyse these changes, the mean vegetation cover and total species numbers were calculated separately for initial species and successional species (Figure 4). A total species number of 19 and a mean vegetation cover of 27.3% were recorded for initial species on plots representing the stage 2 y after the fire event (reference stage). On the plots 4 y after the fire event, 18 of the 19 initial species were also present, but also 18 successional species were recorded. As the number of investigated plots for this time-since-fire category is relatively high (75), the total species number cannot be compared with the other categories. Therefore, to

relativise the data to the minimum sample size, total species numbers are additionally presented as estimates using rarefaction (Figure 4). However, it is important to note that despite almost similar species numbers for initial and successional species on plots 4 y after the fire, their cover values differed substantially (initial species: 42%; successional species: 8.3%). On plots representing 6 y after the fire event, total species numbers declined, and cover values for initial species decreased while they increased for successional species. On plots 8 and 10 y after the fire, the cover values of the initial species stabilised at a high level and the successional species showed relatively low cover values. On plots 12 y after the fire, mean total vegetation cover was highest with more than 60% and the highest number of species was encountered in total (41; 16.3 for rarefaction) and for successional species (28; 8.3 for rarefaction). Fifteen of these successional species were only found on these plots.

#### The relation of the woody layer to time-since-fire

Analysing the woody component of the vegetation revealed no significant relation to time-since-fire for total woody plant abundance or species richness. However, a significant increase in cover values of woody species was observed with time-since-fire. Highest mean cover values were found for 10 and 12 y since fire with  $22.4\% \pm 14.2\%$  and  $21.4\% \pm 15.6\%$ , respectively, compared to 8.6% on sites 2 y after a fire event ( $U = 54.0, P < 0.001$  and  $U = 67.5, P < 0.05$ , respectively).

For assessing the relation between time-since-fire and cover/abundance of single woody species, only *Acacia erioloba*, *Colophospermum mopane*, *Combretum imberbe* and *Pechuel-loeschea leubnitziae* were considered, as they account for 98% of the total abundance (2631 individuals). *Combretum imberbe* showed no significant response to time-since-fire. *Acacia erioloba* showed increasing mean abundance with increasing time-since-fire and highest values after 12 y without fire (Figure 5). As cover values for *Acacia erioloba* showed relatively little response to time-since-fire, the higher abundance values reflect a trend towards higher numbers of small *Acacia erioloba* individuals with time-since-fire. Abundance of *Colophospermum mopane* showed a significant decrease with time-since-fire, with highest values 2 y after fire and lower values on sites with four and more years since the last fire (Figure 5). The calculated ratio between cover and abundance, i.e. the mean area covered per individual showed for *Colophospermum mopane* a linear increase with time-since-fire ( $r^2 = 0.726$ ). Hence, for *Colophospermum mopane* many small individuals were recorded shortly after the fire and significantly fewer, but larger individuals were found on plots with longer time-since-fire. *Pechuel-loeschea leubnitziae* increased in abundance with



**Figure 5.** Mean abundance values for *Acacia erioloba* (a), *Colophospermum mopane* (b) and *Pechuel-loeschea leubnitziae* (c) related to time-since-fire (TSF). The error bars show  $\pm 1$  SD.

time-since-fire (Figure 5). The sites with 12 y since fire showed both maximum mean cover and abundance values. Low mean abundance values were found on plots representing 2 and 4 y after the fire event and lowest values were recorded for 6 and 8 y after the fire. The cover values show a similar trend as the abundance values.

#### The development of species richness with time-since-fire

Species richness was found to be highest soon after the fire event and again 12 y after the fire (Figure 2). For the cover values of *Pechuel-loeschea leubnitziae* a similar development was encountered (Figure 5), while for *Urochloa mosambicensis* a converse trend could be derived (Figure 4). In order to assess the correlation of *Pechuel-loeschea leubnitziae*, *Urochloa mosambicensis* and mean species numbers, Spearman rank correlation was calculated for these three parameters. Species numbers showed a significant positive correlation with the cover

values of *Pechuel-loeschea leubnitziae* ( $r = 0.33$ ,  $P < 0.001$ ) and a significant negative correlation with cover values of *Urochloa mosambicensis* ( $r = -0.39$ ,  $P < 0.001$ ).

## DISCUSSION

### Vegetation changes related to time-since-fire

The approach of analysing species composition and vegetation structure on sites with different time-since-fire can be compared with long-term post-fire monitoring. Although it cannot provide a detailed description of a 'real' development on specific sites, the big advantage of this space-for-time substitution is the possibility for comparative analysis of successional stages after a fire event in a very short time period.

The results of this study show that many species are present in the second year shortly after the fire (referred to in this study as initial species; Figure 2, Figure 4). These initial species usually survive the fire, for instance due to protected buds or as seeds, and have the ability to quickly establish in new habitats. In particular, annual species show relatively high cover values shortly after the fire event. Mean total vegetation cover 2 y after the fire is about 30% and lower than in the following years (*c.* 40%), and predictably also lower than before the fire (Heinl *et al.* 2004). After 4 y without fire, species numbers are relatively high and mean total vegetation cover rises to 40%. This rise in vegetation cover is primarily because of an increase of the initial species and indicates an ongoing recover of these most common species. However, there is a parallel establishment of new species, which were not recorded 2 y after the fire (referred to in this study as successional species; Figure 4).

In subsequent years, total species numbers decline (Figure 2). This can be ascribed to the decline of the annual and short-lived species, which are present in the first years after the fire-event (Figure 3). Accordingly, cover and species numbers for the initial species decline (Figure 4). Finding high species numbers shortly after the fire event followed by a steady decrease of species numbers, which is partially ascribable to the life history of the initial species, strongly supports the concept of post-fire succession (Bond & van Wilgen 1996, Morrison *et al.* 1995).

Six years after the fire, species numbers are low and also the cover values of initial species, which are now most likely represented by just a few perennial species, are low. Few successional species are present, although they show increasing cover values. Most likely only some of the successional species, which were present 4 y after the fire, could establish, and now these species compete with the initial species, reducing their cover and abundance values.

However, 8 y after the fire, cover values of the initial species are high again and the values of the successional species are reduced. In particular, *Urochloa mosambicensis* shows rising cover values over the first 8 y after fire and occupies an increasing portion among the initial species (Figure 4). It is therefore expected that with increasing time-since-fire, a few specific highly competitive species come to dominance, and most of these dominant species are initial species, which survive fires. But obviously also some fire-sensitive successional species are permanently present. Overall, after 8 y without fire, mean species numbers are lowest (Figure 2), successional species decline significantly in cover and abundance and initial species are in principle represented by a few dominant perennial species, especially *Urochloa mosambicensis* (Figure 4).

With 10 y since fire, woody species become more dominant. The long fire-free interval allows especially *Pechuel-loeschea leubnitziae* and *Acacia erioloba* to establish and to grow, as new seedlings and young plants are not suppressed by frequent fires (Bond & van Wilgen 1996, Heinl *et al.* 2007b, Higgins *et al.* 2000). Especially for *Acacia erioloba* relatively high abundance values were recorded after long fire-free periods, which is in line with the documented fire-sensitivity of *Acacia erioloba* (Barnes 2001, Skarpe 1991). *Pechuel-loeschea leubnitziae* shows a similar trend to *Acacia erioloba* and an increase in cover and abundance with time-since-fire, especially after more than 8 y without fire. For *Colophospermum mopane*, in contrast, low cover values were observed in general, except for 2 y after the fire event (Figure 5). These high cover values shortly after the fire might be due to an initial lack of browsing pressure from elephants. Although *Colophospermum mopane* is usually heavily browsed, a significant decrease in browsing activity by elephants after fire has been reported (Ben-Shahar 1993, Kennedy 2000). A short period without elephant browsing after fire would therefore allow the fast-growing shrub to recover and to spread extensively. However, no comparative analyses exist considering the severity of the impact of fire compared with the impact of elephants on *Colophospermum mopane*, which would be necessary to clearly assign the higher cover values to the suppression of elephant browsing by fire.

As *Pechuel-loeschea leubnitziae* accounts by far for the highest cover and abundance values among the woody species (Figure 5), changes in cover and abundance values of this species are expected to have the most significant influence on herbaceous plants. Especially *Urochloa mosambicensis* declines significantly with rising cover and abundance values of *Pechuel-loeschea leubnitziae* (Figure 4), most likely due to competition between these two species. Hence, after 12 y without fire, cover and abundance values of *Acacia erioloba* and *Pechuel-loeschea leubnitziae* are highest, while *Urochloa mosambicensis*

shows relatively low values. Interestingly, mean vegetation cover and total species numbers are also highest 12 y after the fire event, and many new species are found that were not recorded as successional species before.

### Post-fire determinants of species richness

The data show high species numbers shortly after the fire event and 12 y after fire. Lowest species numbers are recorded about 8 y after the fire event. High species richness immediately after fire has been recorded previously for different vegetation types (summarised in Bond & van Wilgen 1996) and is probably due to the favourable conditions of the post-fire environment. The post-fire conditions are usually characterized by high light, high temperatures, high water availability, high levels of nutrients and little competition. As post-fire, both the species of the pre-burn community and previously dormant or suppressed species occur together, relatively high species numbers result (Figure 4; Bond & van Wilgen 1996). With increasing time-since-fire, species numbers decline. This trend is in significant negative correlation with cover values of *Urochloa mosambicensis*. Hence, species numbers are reduced both with time and increasing cover of *Urochloa mosambicensis*, most likely due to competition but also because of the short life span of many of the successional species. However, after more than 10 y, cover values for *Urochloa mosambicensis* are reduced again, as *Pechuel-loeschea leubnitziae* becomes more dominant. As species numbers show a significant positive correlation with the cover values of *Pechuel-loeschea leubnitziae*, highest species richness was found 12 y after the fire-event. Fifteen species in this species pool have not been recorded in earlier time-since-fire stages. The occurrence of these new successional species 12 y after the fire event, which were neither present immediately after the fire nor during the preceding post-fire development, but now appear with the higher cover and abundance of woody species, indicates the creation of new habitats in the vicinity of the established shrubs and trees. Probably by providing shade and protection, new ecological niches are created that are occupied by species which are not typical for floodplains and rather origin from nearby woodland fringes. As these species were not recorded after fire events for many years, they are expected to be fire-sensitive (e.g. *Evolvulus alsinoides*, *Ipomoea coptica*, *Hyphaene petersiana*, *Sesbania* sp.), which could, however, not be documented.

The discussed relation of species numbers with the cover values of *Pechuel-loeschea leubnitziae* and *Urochloa mosambicensis* might not be tied specifically to the development of these two species. Rather the general decline of dominating stoloniferous perennial grass species initiated by the increase of woody species, and

therewith the establishment of new habitats, might be responsible for the changes in species numbers. Overall, species numbers are therefore positively affected by the fire event, negatively by the dominance of high-competitive perennial grass species and again positively by the establishment of new habitats with the occurrence of new woody species. Species richness is therefore favoured by two processes, i.e. both by the fire occurrence and the establishment of woody species. But interestingly, these processes are contradicting, as woody species are usually suppressed by frequent fires (Bond & van Wilgen 1996, Higgins *et al.* 2000). Species richness can therefore neither be optimized by frequent fires nor by fire suppression. Hence, finding high species numbers for short and for long time-since-fire, and different species shortly after the fire event and at late stages of the post-fire succession, indicates the importance of a variety of inter-fire intervals for sustaining species richness and habitat diversity.

#### Drivers of post-fire succession

Post-fire succession is described as different from linear and competitively driven replacement sequences (Bond & van Wilgen 1996). In this concept, post-fire succession is rather cyclical and leads to reoccurring vegetation patterns under a specific fire regime. Species richness is expected to be highest soon after fire (Morrison *et al.* 1995) and succession proceeds by successive elimination of species, with the order of elimination being determined by the relative longevity of the species. The successional change is thus rather driven by the life-history events of the species in relation to disturbance than by their position in the competitive hierarchy (Bond & van Wilgen 1996).

The results of this study only partially support this concept. Species numbers were not highest immediately after the fire event, but rather peak 4 y after fire. This suggests that the importance of survival and the diversity of the seedbank, which can be responsible for high species numbers shortly after fire (Bond & van Wilgen 1996), might be overestimated in the context of post-fire succession (at least for the investigated habitat). Of course, the germination of species immediately after fire is almost exclusively determined by survival and the presence of seeds in the seedbank, but this species pool is apparently smaller than the pool of plant species during the pre-fire period. This is demonstrated by the high number of successional species in this study, which obviously do not contribute to a persistent seedbank. Specific studies on seed persistence of single species and on seedbank diversity in savanna habitats are largely missing, but obviously few species contribute permanently to the seedbank to form the starting point of post-fire succession. The peak in species numbers 4 y after fire is therefore expected to

be due to new colonization of the favourable post-fire environment on the fire scar than due to germination of surviving pre-fire species. Early post-fire succession is not initiated only by the initial species after fire, but largely determined by the ability of species to colonize the fire scar from outside. Thus, the mobility of the savanna species and also the spatial characteristics of the fire scar, i.e. size, shape or patchiness, can become important determinants of early post-fire succession.

Also in regard to the development of the post-fire succession, the present study can only partially support the above-mentioned concept of a post-fire succession, which is based on the life history of the initial species after fire (Bond & van Wilgen 1996, Morrison *et al.* 1995). This 'typical' fire succession was only observed for the first 8 y after fire. In accordance with their life history, cover values of short-lived species declined progressively with time-since-fire, while cover values of perennial grass species (e.g. *Urochloa mosambicensis*) increased. The observed dominance of the perennial grass species after about 8 y should theoretically persist until the next disturbance event (e.g. fire) – but could also be broken by competition. The latter was observed in this study. About 10 y after the fire event, *Urochloa mosambicensis* decreased, while woody species increased (especially *Pechuel-loeschea leubnitziae*) – both independent of the fire event. This significant negative interaction between those species, but also the differences in the species pool a few years after fire compared with 12 y after fire, indicate a change in the driving forces of post-fire succession with time-since-fire. Late post-fire succession is predominantly driven by competition and niche differentiation (competition-driven) and less by life-history events of the species in relation to fire (fire-driven).

One might argue that a time span of more than 10 y is too long to discuss succession in fire-prone savanna habitats still in a post-fire context. But fire-return-intervals of more than 10 y are not unusual for savanna habitats (Heinl *et al.* 2006, van Wilgen & Scholes 1997). However, independent of a definite fire-return interval, the timing of fire-driven and competition-driven sequences in the post-fire succession might be crucial for savanna dynamics and any kind of fire management. Fire events during fire-driven sequences might lead to a rather stable and recurring species structure and composition, primarily based on survival, seedbank dynamics and colonisation. Longer fire-free windows, however, allow for competitively driven shifts in species dominance and eventually for the establishment of new species (e.g. in the vicinity of woody species). And this would not only lead to changes in plant communities, but could also alter the fire-sensitivity or flammability of the vegetation and in consequence also the fire regime.

The transition from fire-driven to competition-driven post-fire succession is definitely fluid and varies with



the habitat type. Specific time spans for the successional sequences can therefore not be formulated. However, the differentiation of post-fire successional stages, as shown in the present study, is obviously crucial for assessing and understanding ecological effects of fire in savanna habitats.

## ACKNOWLEDGEMENTS

The studies were conducted in the scope of the project 'Fire regime and vegetation response in the Okavango Delta, Botswana' funded by Volkswagen Foundation, Germany with support from Conservation International Botswana, Okavango Program. Special thanks to Professor Lars Ramberg and the staff of the Harry Oppenheimer Okavango Research Centre in Maun, to Professor George Bredenkamp (University of Pretoria, South Africa) and to Professor Jörg Pfadenhauer (Technische Universität München, Germany) for scientific support.

## LITERATURE CITED

- ANDERSEN, A. N., BRAITHWAITE, R. W., COOK, G. D., CORBETT, L. K., WILLIAMS, R. J., DOUGLAS, M. M., GILL, A. M., SETTERFIELD, S. A. & MULLER, W. J. 1998. Fire research for conservation management in tropical savannas: introducing the Kapalga fire experiment. *Australian Journal of Ecology* 23:95–110.
- ARNOLD, T. H. & DE WET, B. C. 1993. *Plants of Southern Africa: names and distribution*. Memoirs of the Botanical Survey of South Africa No. 62; Botanical Research Institute, Pretoria.
- BARNES, M. E. 2001. Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology* 39:340–350.
- BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65:249–256.
- BOND, W. J. 1997. Fire. Pp. 421–446 in Cowling, R. M., Richardson, D. M. & Pierce, S. M. (eds.). *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- BOND, W. J. & VAN WILGEN, B. W. 1996. *Fire and plants*. Population and Community Biology Series 14. Chapman & Hall, London. 263 pp.
- BOOYSEN, P. D. V. & TAINTON, N. M. 1984. *Ecological effects of fire in South African ecosystems*. Ecological Studies 48, Springer-Verlag, Berlin.
- DEBANO, L. F., NEARY, D. G. & FOLLIOTT, P. F. 1998. *Fire's effects on ecosystems*. Wiley and Sons, Inc., New York. 333 pp.
- ELLERY, K. & ELLERY, W. 1997. *Plants of the Okavango Delta – a field guide*. Tsaro Publishers, Dalbridge. 225 pp.
- GIBBS-RUSSELL, G. E., WATSON, L., KOEKEMOER, M., SMOOK, L., BARKER, N. P., ANDERSON, H. M. & DALLWITZ, M. J. 1990. *Grasses of Southern Africa*. Memoirs of the Botanical Survey of South Africa, No. 58, National Botanical Institute, Pretoria.
- HEINL, M., SLIVA, J. & TACHEBA, B. 2004. Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana. *South African Journal of Botany* 70:695–704.
- HEINL, M., NEUENSCHWANDER, A., SLIVA, J. & VANDERPOST, C. 2006. Interactions between fire and flooding in the Okavango Delta floodplains, Botswana. *Landscape Ecology* 21:699–709.
- HEINL, M., FROST, P., VANDERPOST, C. & SLIVA, J. 2007a. Fire activity on floodplains and drylands in the Okavango Delta, Botswana. *Journal of Arid Environments* 68:77–87.
- HEINL, M., SLIVA, J., TACHEBA, B. & MURRAY-HUDSON, M. 2007b. Vegetation response to fire frequency in the Okavango Delta floodplains, Botswana. *African Journal of Ecology* (in press).
- HIGGINS, S. I., BOND, W. J. & TROLLOPE, W. S. W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213–229.
- KENNEDY, A. D. 2000. Notes and records – wildfire reduces elephant herbivory on *Colophospermum mopane* (Fabaceae). *African Journal of Ecology* 38:175–177.
- KREBS, C. J. 1999. *Ecological methodology*. Benjamin Cummings, California. 624 pp.
- LONDO, G. 1984. The decimal scale for relevés of permanent quadrats. Pp. 45–49 in Knapp, R. (ed.). *Sampling methods and taxon analysis in vegetation science*. Handbook of Vegetation Science (4). Junk Publishers, The Hague.
- MCCARTHY, T. S., COOPER, G. R. J., TYSON, R. D. & ELLERY, W. N. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science* 96:25–32.
- MORRISON, D. A., CARY, G. J., PENGELLY, S. M., ROSS, D. G., MULLINS, B. J., THOMAS, C. R. & ANDERSON, T. S. 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology* 20:239–247.
- SKARPE, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* 2:565–572.
- VAN OUDTSHOORN, F. 1999. *Guide to grasses of Southern Africa*. Briza Publications, Pretoria. 288 pp.
- VAN WILGEN, B. W. & SCHOLES, R. J. 1997. The vegetation and fire regimes of southern hemisphere Africa. Pp. 27–46 in van Wilgen, B. W., Andrae, M. O., Goldammer, J. G. & Lindsay, J. A. (eds.). *Fire in Southern African savannas*. Witwatersrand University Press, Johannesburg.